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Rarely naturalized, but widespread and even invasive: the paradox of a popular pet terrapin expansion in Eurasia

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Abstract

The North American terrapin, the red-eared slider, has globally recognized invasive status. We built a new extensive database using our own original and literature data on the ecology of this reptile, representing information on 1477 water bodies throughout Eurasia over the last 50 years. The analysis reveals regions of earliest introductions and long-term spatio-temporal dynamics of the expansion covering now 68 Eurasian countries, including eight countries reported here for the first time. We established also long-term trends in terms of numbers of terrapins per aquatic site, habitat occupation, and reproduction success. Our investigation has revealed differences in the ecology of the red-eared slider in different parts of Eurasia. The most prominent expression of diverse signs of invasion success (higher portion of inhabited natural water bodies, higher number of individuals per water body, successful overwintering, occurrence of juvenile individuals, successful reproduction, and establishment of populations) are typical for Europe, West Asia and East Asia and tend to be restricted to coastal regions and islands. Reproduction records coincide well with the predicted potential range based on climatic requirements but records of successful wintering have a wider distribution. This invader provides an excellent and possibly unique (among animals) example of wide alien distribution, without the establishment of reproducing populations, but through the recruitment of new individuals to rising pseudopopulations due to additional releases. Therefore, alongside the potential reproduction range, a cost-effective strategy for population control must take in account the geographical area of successful wintering.

Graphical abstract

Keywords
Alien species, biological invasions, global change, invasion ecology, nature conservation, wintering

Introduction

The growth of the global human population and the development of international transport networks has resulted in mass translocations of biological species outside of their native ranges, that have led to the homogenization of the Earth's biota within potential ecological niches (McKinney and Lockwood 1999; Seebens et al. 2020). Intentional and unintentional biological invasions represent considerable issues for native biodiversity, economic activities and even human health (Gilpin 1990; Vitousek et al. 1996; Mazza et al. 2014).

The invasion of alien amphibians and reptiles has significantly accelerated since the middle of 20th century (Kraus 2009; Capinha et al. 2017). Alongside the brahminy blindsnake *Indotyphlops braminus* and common house gecko *Hemidactylus frenatus*, the

pond slider *Trachemys scripta* (Schoepff, 1792) is one of the three most widespread alien reptiles globally (Capinha et al. 2017). The native range of the pond slider *Trachemys scripta* is restricted to central, southern and southeastern United States and the adjacent portion of Mexico (Rhodin et al. 2017). This species of terrapin consists of at least three subspecies. Subspecies *T. s. scripta* (yellow-bellied slider) and *T. s. troostii* (Cumberland slider) are kept and bred in captivity substantially less often compared with *T. s. elegans* (red-eared slider). The last taxon became very popular as a pet animal, sometimes also an ornamental pond animal, and has been one of the most-traded reptiles since the middle of the 20th century. Export from the United States to other countries reached millions of individuals per year (Telecky 2001; Reed and Gibbons 2003). Since the end of 20th century, large-scale commercial breeding of *T. s. elegans* also started in China and countries of Southeast Asia where it is used for human consumption (van Dijk et al. 2000). These active and mobile reptiles often escape captivity.

Young red-eared slider individuals are small and brightly colored, making them very attractive for aquarists. However, these animals grow rapidly, and large individuals require more space, are less visually appealing, aggressive and may bite. Releasing them into the nearest water body is a common way to get rid of an annoying pet. This terrapin easily adapts to outdoor conditions and can reproduce and establish stable populations in regions with an appropriate climate (Rödder et al. 2009; Heidy Kikillus et al. 2010). Once established, the slider may induce a negative impact on native macrophytes and hydrobionts (Ficetola et al. 2012). Amphibians are regarded to be especially vulnerable because this terrapin feeds on tadpoles, and the presence of chemical cues released by this predator can affect the development rate and size at metamorphosis of tadpoles (Polo-Cavia et al. 2010; Vodrážková et al. 2020). The red-eared slider is more aggressive and has higher reproductive characteristics and, hence, may successfully compete with native terrapin species for food, basking sites and, possibly, egg-laying places (Cadi and Joly 2003; Perez-Santigosa et al. 2008; Pérez-Santigosa et al. 2011; Polo-Cavia et al. 2011; Pearson et al. 2015). Experimental studies have confirmed a higher mortality of native European pond terrapin in the presence of the invasive red-eared slider (Cadi and Joly 2004). In addition, this alien terrapin can induce the genetic pollution of populations of native terrapins due to introgression (Parham et al. 2013) and is involved in the life cycles of native parasite species, while also acting as a vector for the invasion of alien parasites, which are capable of infecting native terrapins and increase the risk of epizootics, causing mass mortalities (Iglesias et al. 2015; Demkowska-Kutrzepa et al. 2018). Moreover, this alien reptile can carry the agents of salmonellosis, which is dangerous for human health (Nagano et al. 2006; Shen et al. 2011). For these reasons, the trade of small-sized (<10 cm) individuals of red-eared slider was banned in the 1970s in the United States and import of this reptile to Europe has been entirely banned since 1997 (Ficetola et al. 2012).

Despite biosecurity efforts in some countries, today the pond slider (mainly red-eared slider) occurs in outdoor water bodies on all continents except Antarctica

(Ramsay et al. 2007; Ficetola et al. 2012; Rhodin et al. 2017). The invasive ranges of the pond slider *T. scripta* and its subspecies *T. s. elegans* in some regions of Eurasia were recently reflected in several scientific reviews (Sillero et al. 2014; Rhodin et al. 2017). However, regions of Eurasia significantly differ in volumes of primary data. The best studied region is West Europe (Sillero et al. 2014) whereas huge areas of North Asia, South Asia, and Middle and Central Asia (marked below as Central Asia) are commonly depicted as a blank spot, reflecting the absence of appropriate studies (Rödder et al. 2009; Heidy Kikillus et al. 2010; Ma and Shi 2017; Rhodin et al. 2017). Detecting the alien terrapins is easy in park ponds during warm seasons but may be a difficult task when direct spotting is limited by seasonality, weather (especially in northern regions), large water body size, macrophyte densities, and landscape features. In those cases, indirect express methods of detection, such as detection dogs, e-DNA or parasitological analysis of co-inhabiting hydrobionts, may be applied (O'Keeffe 2009; Kakuda et al. 2019; Reshetnikov and Sokolov 2020).

Modelling of potential ranges of species is a popular direction of contemporary ecology; analyses have been performed for the red-eared slider, mainly at the species level using available datasets and on different geographic scales (e.g., Ficetola et al. 2009; Rödder et al. 2009; Heidy Kikillus et al. 2010; Masin et al. 2014; Banha et al. 2017). However, physiological differences of subspecies are debatable and individuals of other subspecies are less common in regions outside their native distribution. Importantly, additional primary data from extensive, previously unstudied, regions can alter knowledge about its niche and, hence, its potential distribution.

Different definitions of the term "invasive species" have been proposed based on ecological and/or practical approaches (e.g., Jeschke and Strayer 2005; Beck et al. 2008; Blackburn et al. 2011). We suggest that the main features of an invasive alien taxon are establishment of self-sustaining populations and their significant effect on native ecosystems. Due to assumed negative influences on freshwater ecosystems, the widely spread subspecies *T. s. elegans*, is regarded as an invasive taxon in Europe and North Asia (European Commission 2016; Reshetnikov et al. 2018). However, despite the large volume of scientific publications on this animal, to date, data on negative impact of the red-eared slider upon native species are scarce in most regions of Eurasia (but see: Cadi et al. 2004; Perez-Santigosa et al. 2008) and geographic limits of its invasive populations are still debatable because confirmation of its successful reproduction is a complex task (Cadi and Joly 2004). We hypothesized that the invasion ecology, including establishment of populations, of this reptile in different colonized areas may differ and thus the invasive status of red-eared slider needs to be reviewed. A distinguishing feature of our investigation is the use of an integrated comprehensive database, with primary data collected by professional herpetologists from previously non-studied regions. Here, we aimed to analyze the invasion ecology of this alien reptile in different parts of Eurasia, establishing foundations for the verification of its invasive status and for an update of current biosecurity approaches.

Materials and methods

Data collection

For assessing the current distribution, the verified original records of the red-eared slider from 236 geographic localities were collected by the authors of this paper during their field inspections of water bodies in different regions of Eurasia in 2002–2020. Additionally, 1241 relevant records from 1968–2020 were obtained from scientific papers (Suppl. material 1), however 99.4% of these literature records are from 1990 and later, and 96.1% are from 2000 and later. All original data were subjected to rigorous verification. In doubtful cases, i.e., without georeferenced location or exact identification of terrapins by authors of observations, we requested and analyzed the coordinates of the localities, and photos with details of head and neck coloration for correct identification. The identity of 167 inconclusive cases (not included in the above-mentioned numbers) was not confirmed and they were therefore not included in the analysis. We also used two datasets (for Europe and Asia) from the Global Biodiversity Information Facility (GBIF; www.gbif.org) with records from 1978–2020. Assuming red-eared slider is an invasive taxon with described remarkable impact on native species (Cadi et al. 2004; Perez-Santigosa et al. 2008), and keeping in mind the absence of data on its impacts for the majority of the georeferenced records, we analyzed all above-mentioned data regardless of impact. The data were structured into categories depending on the source of data (original/literature/GBIF) and identification level (species/subspecies). We did not include in the analysis the available data on the presence of red-eared sliders in open water bodies on territories of zoological parks (e.g., Rupperswil, Klagenfurt, Belgrade, Sofia, Odessa, Moscow, Rostov-on-Don, Barnaul, Singapore, Izmir, Istanbul, Mersin, Antalya) because of likely management and care by staff (i.e., artificial wintering of adult terrapins, special conditions for egg incubation), but we used data from other urban parks. The original and literature records of the red-eared slider were distributed as follows: 713 in Europe, 589 in East Asia, 21 in North Asia, 61 in West Asia, 4 in Central Asia, 50 in South Asia, 39 in Southeast Asia (see Suppl. material 2 for delineation of the continent). The database of original and literature records is available in Suppl. material 3. The data from GBIF represented 5967 records from Europe and 31 records from Asia. Altogether, 1477 original/literature records and 5998 records from GBIF of *T. s. elegans* were included in the analysis (Fig. 1a).

Terminology

We used earlier suggested terms (Reshetnikov 2013) for discussion of the invasion process: a. initial introduction; b. center (source) of the secondary distribution, i.e., the region invaded by the alien species around the point of initial introduction serving as a source for further expansion; c. invaded subrange, i.e., part of the invaded range assumed to have originated from a single or a limited number of initial introductions, geographically separated from other invaded subranges, which may be temporally separated and later merged. Commonly, these processes are identified through the spatio-temporal analysis of records but additional tools, such as molecular-genetic methods, are also important.

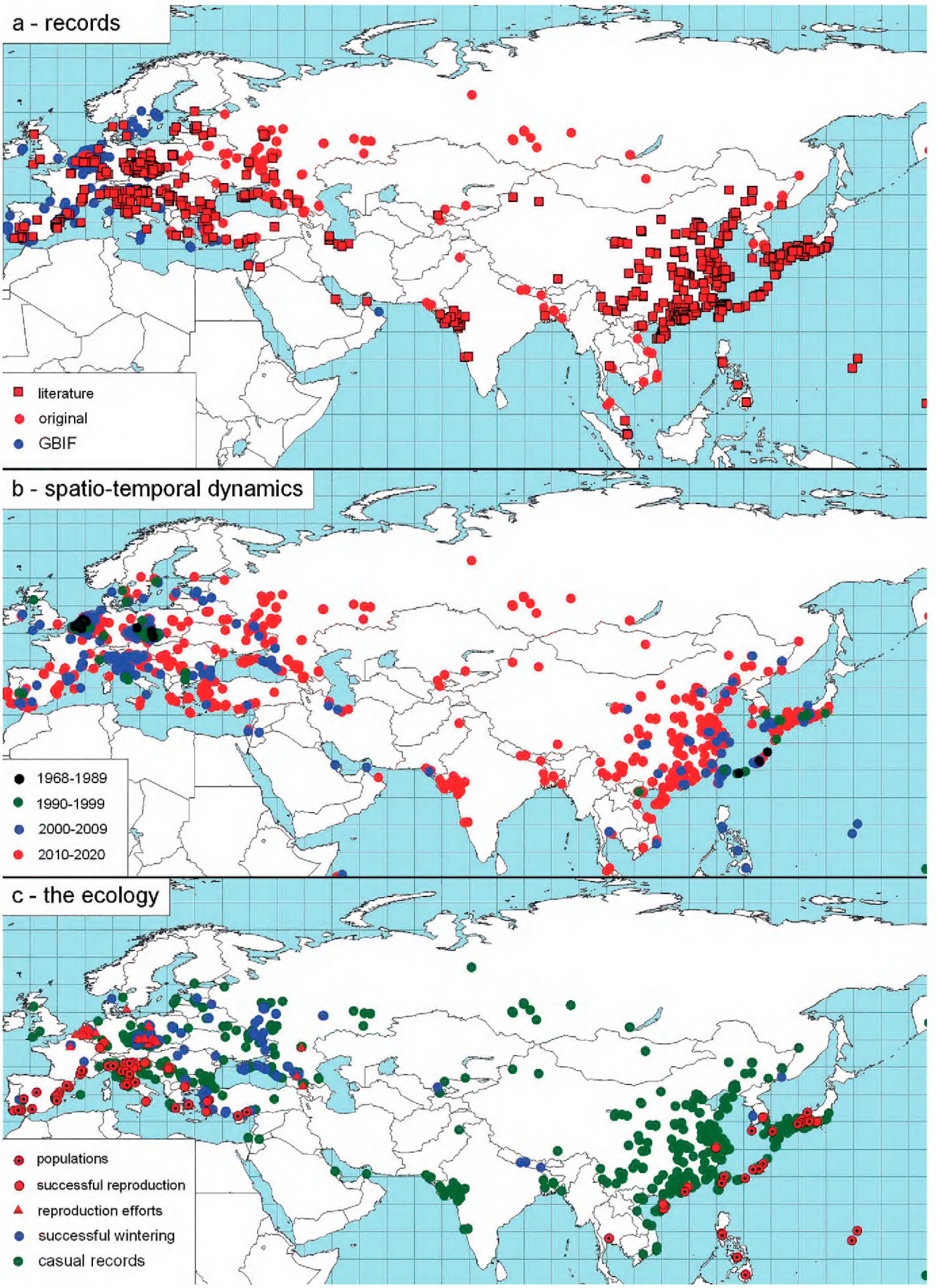


Figure 1. The geographical distribution of the red-eared slider *Trachemys scripta elegans* in Eurasia. **a** sources of data: 1 (red squares) – records from literature sources (see Suppl. material 1); 2 (red circles) – original records; 3 (blue circles) – records from GBIF.org (12 September 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.4qk7b3; https://doi.org/10.15468/dl.tppua3. The layers are located from 1 (above) to 3 (below) **b** spatio-temporal dynamics of records: 1 (black circles) – records of 1968–1989; 2 (green circles) – records of 1990–1999; 3 (blue circles) – records of 2000–2009; 4 (red circles) – records of 2010–2020. The layers are located from 1 (above) to 4 (below); **c** the ecology: 1 (red circles with dot) – records of established populations; 2 (red circles) – confirmed successful reproduction; 3 (red triangles) – unsuccessful reproduction attempts; 4 (blue circles) – confirmed successful overwintering; 5 (green circles) – records without information on ecology. The layers are located from 1 (above) to 5 (below).

Habitats, number of terrapins per water body, body sizes and ecology

We used all available georeferenced data (1968–2020) to understand the invasion ecology of this reptile in regions of Eurasia. Some original and literature records indicated habitat characteristics (N=1219), number of sliders per water body (N=963), measure of slider sizes (carapace length, CL, with accuracy ± 1cm) and/or distant assessing of sizes (with an interval of 5cm) (N=570), and information on ecology (N=270). The proportion of records with appropriate data are presented for each part of Eurasia separately in Table 1.

Table 1. Proportion of records (%) with appropriate data for each part of Eurasia.

	Europe	E Asia	N Asia	W Asia	S Asia	SE Asia	C Asia
Habitats	82.3	89.8	100	83.6	24.0	38.5	100
Numbers	75.3	54.5	95.2	93.4	22.0	33.3	100
Sizes	33.1	40.7	85.7	78.7	26.0	35.9	25
Ecology	26.2	6.1	4.8	50.8	6.0	28.2	100

We used data on latitude, longitude, date, habitat characteristics, number of individuals per water body, body sizes, and ecology to build correlation matrixes. Some parameters (habitat characteristics, body sizes, and ecology) were ranked as presented in Suppl. material 4. To assess the degree of synanthropy we used the above-mentioned data on habitats as continuing transition from habitats outside human settlements (lowest synanthropy) to recreational parks (highest synanthropization). When calculating relationships with sizes, we ignored scores "6" and "7" ("adults", "all sizes") as well as cases with several different sizes in the same water body. To build a histogram with body sizes, we included cases with several different sizes in the same water body (e.g., 1, 3 or 2, 3, 4); they were counted as separate cases of observations. Therefore, contrary to correlation analysis, the histogram with size classes represents analysis of cases of observations but not of water bodies. For assessment of the degree of reproduction success, we used data on ecology (see Suppl. material 4) after excluding score "1" ("casual records"). Therefore, the reproduction scale represents a continuum from just successful overwintering to established populations.

Species distribution models

We aimed to build two species distribution models (SDM) for red-eared slider: (a) the potential range of successful reproduction as an assessment of the probable area of population establishment (SDM1); (b) the potential range of successful overwintering as a probable area of long-term survival of released individuals (SDM2). The models were built using four sequential steps: (i) preparation of vector and raster layers; (ii) thinning of environmental variables and georeferenced records; (iii) selection of background areas for MaxEnt models; (iv) determination of MaxEnt model parameters; (v) building SDMs using MaxEnt.

i. Preparation of vector and raster layers. Vector layers of occurrence records were created in ArcGis 10.6.1 (Environmental Systems Research Institute 2020) using the full number of available records (9204 records: 1729 in the native and 7475 in Eurasian invasive parts of the slider range). Bioclimatic variables (all 19) were obtained from the WorldClim 2.1 dataset (Hijmans et al. 2005). In addition to this dataset, we also analyzed 16 predictor variables from the ENVIREM dataset (Title and Bemmels 2018), many of which are related to the ecology of the terrapin under study. Thus, we created raster layers for 35 environmental variables at a spatial resolution of 2.5 arc minutes (~5 km^2) for further analysis. This stage was common for both (SDM1 and SDM2) models.

ii. Thinning of environmental variables and georeferenced records. We tested for mulicollinearity amongst the potential predictor variables using two methods: the Pearson correlation coefficient, with a threshold value of > 0.75; and the variation inflation factor (VIF), with a threshold value of > 10 (Hair et al. 1995). The corSelect function in the fuzzySim package (Barbosa 2015) was used for these analyses. Based on these results, and the ecological requirements of the red-eared slider, we selected four predictor variables that were used in the SDMs. The selected four variables, their descriptions and links to slider ecology are as follows:

- BIO10 (defined as the mean temperature of the warmest quarter). This variable represents the availability of thermal energy, particularly for feeding activity, and was included because the northern distribution of red-eared sliders may be limited by low summer temperatures. This species requires water temperatures higher than 10 °C for the activation of feeding behavior, while the optimal soil temperature for embryonic development of eggs is 26–32 °C (Parmenter 1980).
- growingDegDays0 (defined as the sum of mean monthly temperature for months with mean temperature greater than 0 °C, multiplied by the number of days in that month). This variable reflects the duration of the ice-covered period, i.e., time without access to air oxygen. Red-eared sliders are assumed to have limited ability for long-term survival under anoxic conditions (Ultsch 2006).
- BIO18 (defined as levels of precipitation during the warmest quarter). This variable may be important for humidity-dependent embryonic development of skin-shelled eggs of red-eared sliders (Tucker et al. 1998).
- climaticMoistureIndex (defined as a metric of relative wetness and aridity). This variable is related to water availability and hence is a key factor for the stability of aquatic habitats (shallow water bodies), which may shrink during summer.

In our case, the maximum Pearson coefficient was PC=0.742 between the variables BIO10 and growingdegdays0, and the maximum VIF=6.8 for the variable BIO10.

We used a two-step procedure to identify and reduce the spatial autocorrelation of georeferenced records. We used the spThin package in R (Aiello-Lammens et al. 2015) to subsample the data ten times, using ten thinning parameters – the records were separated by distances of 10–100 km in intervals of 10 km. Then the ten datasets were subjected to a cluster analysis using the average nearest neighbor index (ANNI) in ArcGis 10.6.1 (Environmental Systems Research Institute 2020). After this

analysis, we chose the set of georeferenced records for which ANNI=1. As a result of this approach, we obtained a reduced dataset which was used for preparation of two datasets (DS1, DS2) for creating two bioclimatic models (SDM1, SDM2) accordingly (Suppl. material 6): the potential range of successful reproduction as an assessment of the probable area of population establishment (SDM1); the potential range of successful overwintering as a probable area of long-term survival of released individuals (SDM2). The first model was built based on georeferenced records (DS1) from the native range of the species in North America, taken from the International database GBIF (n=373 from GBIF.org (29 July 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.d88pay; we verified this dataset by comparing with the native range of *T. s. elegans* reported in Rhodin et al. 2017) and Eurasian original and literature records of successful reproduction and established populations (n=98). The second model, i.e., wintering range, was based on DS2 which included the above-mentioned datasets, with the addition of records of confirmed successful overwintering within Eurasia (n=124).

iii. Selection of background areas for MaxEnt models. We used the conventional choice of background localities from the presence region, here defined as the convex polygon, to build the two models (Rodda et al. 2011). However, the conventional choice of background localities in convex polygon may have some limitations as this minimizes the contrast between presence and absence, so we employed the recommendations presented in previous literature (Lobo et al. 2008; Lobo et al. 2010). These studies suggest selecting backgrounds from areas that are immediately adjacent to occupied habitats but are known to be unoccupied. For this reason, we combined convex polygons located in North America, southern Europe, East Asia, and Southeast Asia, which included appropriate georeferenced records. Background areas for the two models are presented in Suppl. material 6.

iv. Determination of MaxEnt model parameters. Although the SDMs built with MaxEnt (MaxEnt.jar; Dismo) (Phillips and Dudík 2008; Hijmans et al. 2017) using default parameters were based on extensive empirical material, some studies have shown that they can be inefficient (e.g., Muscarella et al. 2014). For this reason, we determined the optimal MaxEnt model parameters for each type of model using the AICc information criterion in the ENMeval R package (Muscarella et al. 2014). ENMeval applies three threshold-independent evaluation metrics: AUC_{Test}, AUC_{Diff}, and the size-corrected Akaike information criterion (AICc). AUC_{Test} is a metric that measures the discriminative ability of an SDM using georeferenced records that were not used when the model was built. AUC_{Diff} is the difference between the AUC calculated from the AUC_{Train} training sample and AUC_{Test}. This metric (AUC_{Diff}) is a measure of model overtraining. AICc, adjusted for small sample size, reflects the degree of fit and complexity (Muscarella et al. 2014; Guisan et al. 2017; Title and Bemmels 2018). The ENMeval package creates a number of MaxEnt models for each dataset using different regularization multiplier (RM) values and feature classes (FC), compares them using the AICc criterion and chooses the most appropriate model. This package typically selects a model that is less complex than the default model adopted by MaxEnt, with acceptable AUC_{Train} and AUC_{Diff} metrics (Halvorsen et al. 2016; Title and Bemmels 2018). Although we did not find any general trends in the selection of

FC, the FCs selected using the AICc models had higher RM values than the default value of 1.0 (Suppl. material 7). As a result, the following parameters were chosen for SDM1: feature classes (L = linear, Q = quadratic), and RM=4.0. For SDM2- feature classes (L = linear, Q = quadratic, H = hinge, P =product and T = threshold), and RM=4.0 (see Suppl. material 7)

v. Building SDMs using MaxEnt. Species distribution models were built using the maximum entropy method by MaxEnt 3.4.1 with optimal MaxEnt parameters (Hijmans et al. 2017). When training the models, we used occurrence records and background areas as presented in Suppl. material 6. We used a 'sre' strategy for the random generation of the background (pseudo-absence) (PA) points using the Biomod v.2.0 R package. The number of PA points generated (as recommended by Barbet-Massin et al. 2012) was according to the number (N) of georeferenced records (if N ≤ 1000 then 1000 points were selected, otherwise 10,000 points were selected). At the next stage, we projected the MaxEnt models with optimal parameters onto the territory of Eurasia. Final versions of these models were built as a result of 10 MaxEnt runs to randomly select test and training georeferenced records. In all MaxEnt runs, 80% of the records were used as training samples while 20% served as test samples. We used the Boyce index (Bind) to assess model performance (Boyce et al. 2002; Di Cola et al. 2017), with the help of the EcoSpat R package (Di Cola et al. 2017). The Boyce index lacks the drawbacks present in the AUC index (Lobo et al. 2008; Guisan et al. 2017; Petrosyan et al. 2020).

Analysis of niches

To analyze the features of environmental factors favorable for successful reproduction of the studied terrapin, a comparative analysis of the centroids (mean positions of species localities in relation to environmental factors) of niches for several predictor variables in three parts of the range (Europe, West Asia, and East Asia) was carried out. These parts of the range were selected because of sufficient records of four ecological characteristics: confirmed successful overwintering, unsuccessful reproduction attempts, confirmed successful reproduction, and established populations. Comparative analysis was performed using GLM ANOVA (see section Statistics) based on raw values of ecologically important predictor variables (BIO10, BIO18, growingDegDays0, climaticMoistureIndex the same as used for the SDMs – see the methodology above).

Statistics

Normalized histograms were used for visualization of data on invasion ecology; means and standard errors are shown in the text as descriptive statistics. Spearman R rank correlation coefficient was applied for assessing possible relationships between measures of invasion ecology, date, and latitude and longitude. Statistical hypotheses were tested at 0.05 *p*-level. Multiple comparisons of the proportion of key habitat use by the red-eared slider in the three parts of the invaded range (Europe, West Asia, East Asia) for which there were enough data for appropriate statistical analysis was performed using

the chi-square statistical test and then the Tukey Post hoc test (Zar 2010). In addition, we also used the Shannon's index to assess body size diversity in these parts of the range. A comparative analysis of Shannon's indices for size diversity was made using the test proposed by Hutcheson (Magurran 1988).

Comparative analysis of niche centroids was made using the Generalized Linear Model (GLM) procedure. In this model, one way analysis of variance (ANOVA) was used with equal and unequal numbers of replicates in the cells. In all cases, type I analysis of variance models was used, i.e., fixed factor models. In the first ANOVA model we used the factor "geographic region" and compared species niche centroids (means of predictor variables) in different geographic regions (Europe, West Asia, and East Asia), i.e. we used one-way ANOVA with three levels of region factors. For the second group of the models, the factor "establishment success" was used, consisting of four levels of reproductive/establishment status (see above). This analysis is important to identify the range of environmental parameters favorable for successful reproduction. If an analysis of variance with fixed effects showed a significant difference in the level of factors, a test of multiple comparison, the Post hoc Tukey HSD was used to determine which levels of the factor differed from each other. For multiple comparisons with unequal variances according to Leuven's test, the Tukey-Cramer test with Welch's modification was used (Zar 2010). Prior to the analysis, all data were Log-transformed to achieve normal distribution of the GLM ANOVA residuals. This additional analysis is important because it allows us to test the validity of GLM ANOVA results using non-transformed data with residuals that differ from the normal distribution, as recommended in the literature (Zar 2010).

Statistical analysis was performed using basic and special packages in the R language in RStudio Version 1.2.5033 (RStudio Team 2020). We used MaxEnt.jar and a set of R packages spThin (Aiello-Lammens et al. 2015), ENMeval (Muscarella et al. 2014), EcoSpat (Di Cola et al. 2017), Biomod2 (Thuiller et al. 2021), Raster (Hijmans et al. 2022), Dismo (Hijmans et al. 2017), fuzzySim (Barbosa 2015) in RStudio Version 1.2.5033 (RStudio Team 2020) to build SDM models. In addition, we also used ArcGis 10.6.1 (Environmental Systems Research Institute 2020) to prepare raster layers of predictor variables, analyze the average nearest neighbor index, and visualize SDMs.

Results

Spatio-temporal dynamics and current occurrence range in Eurasia

Records from 1968–1989 fall into countries in Europe, West Asia, and East Asia. The earliest records were reported from the Czech Republic from 1968, southern Japanese islands from 1972, Israel from 1975, the Netherlands from 1980, and Belgium from 1982. Records from 1990–1999 occurred in more regions of Europe, West Asia, East Asia and expanded to Southeast Asia (the Czech Republic, Spain, Italy, Sweden, England, Romania, Germany, Belgium, the Netherlands, Poland, Israel, Japan, Thailand, Vietnam, Republic of Korea and the Taiwan Island). By 2010

this reptile was already known in all parts of Eurasia, except Central Asia and North Asia, but today it occurs in all parts of Eurasia. Spatio-temporal dynamics of records are shown in Fig. 1b.

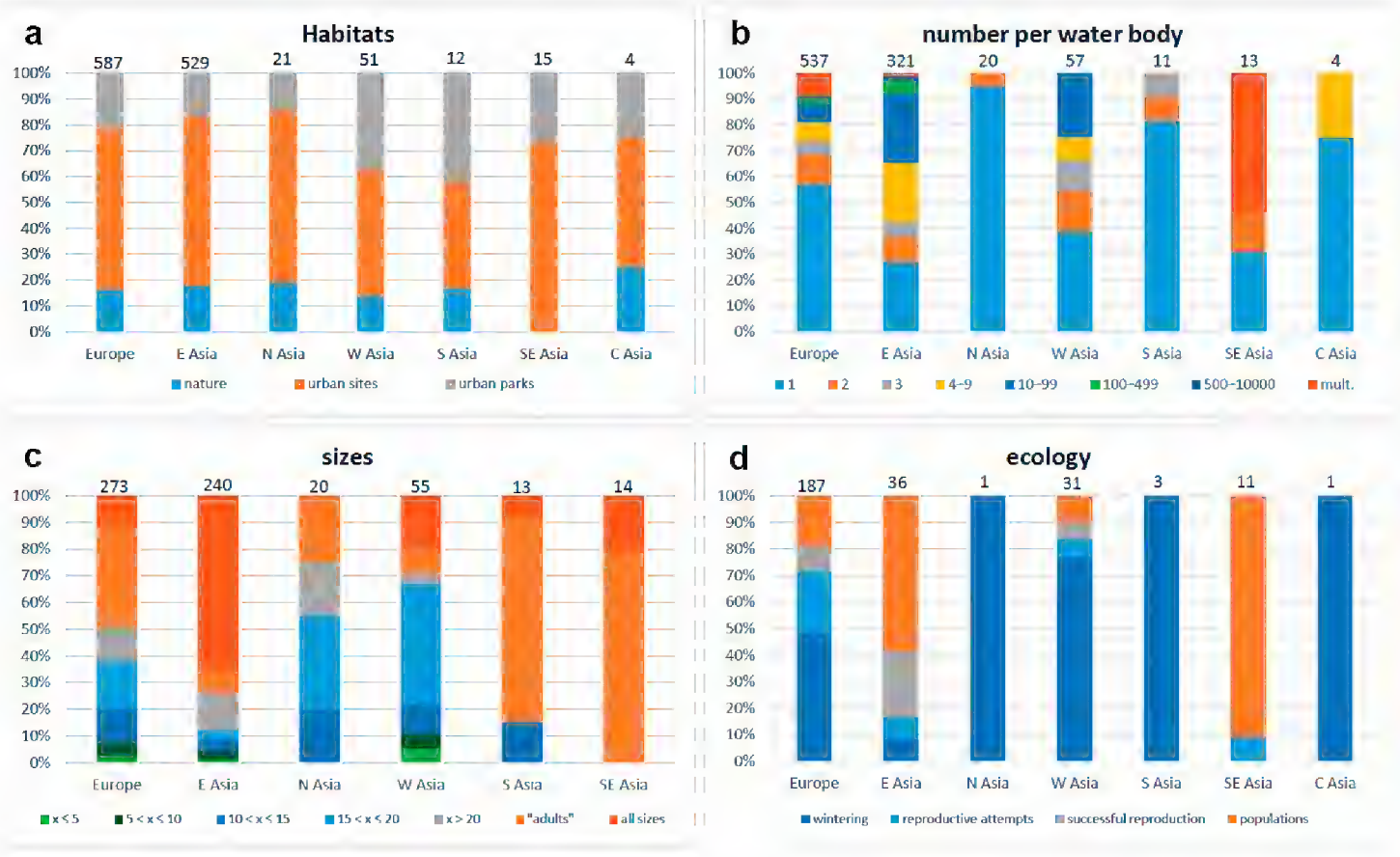
Synanthropy

In the most studied parts of the continent, i.e., Europe and East Asia, the proportion of records in parks and other urban environments reaches 83.8 and 82.6% respectively (Fig. 2a). In West Asia, with 51 appropriate observations, records in human settlements reach 86.3% (Fig. 2a). In Europe, synanthropy of the red-eared slider is more typical for eastern regions (see Suppl. material 5). Despite the general assessment that synanthropy did not correlate to latitude (see Suppl. material 5), records of the terrapin outside urban territories and rural settlements (score 1) highlighted a negative correlation with latitude values in Europe ($R = -0.10$; $t(n-2) = -2.41$; $N = 587$; $p<0.05$) and a positive correlation with reproduction success ($R = 0.20$; $t(n-2) = 2.36$; $N = 135$; $p<0.05$). In Europe, more synanthropic groups of terrapins are more abundant (higher number of individuals per water body), and portion of registered synanthropic groups has increased over the years. In East Asia, synanthropy is less common in southern regions and, similarly to Europe, has increased over the years. In West Asia, more synanthropic groups are more abundant (see Suppl. material 5).

Distribution of red-eared sliders among the three types of habitats does not differ between the European and East Asian parts of the range, but habitat distribution in both regions significantly differe from habitat distribution in West Asia (Fig. 3). Remarkably, in all parts of the studied range, the proportion of records in the second habitat, i.e., records located in water bodies within human settlements but outside recreational areas, is significantly greater than that of habitats 1 and 3, sites outside human settlements and public parks (Fig. 3). In West Asia, the studied terrapin is found significantly more often in parks and other recreational areas (Fig. 3) compared with Europe and East Asia. The proportion of records in habitat 2 (Fig. 3) in West Asia is significantly less than in Europe and East Asia. The proportion of records in nature environments (habitat 1), i.e., outside human settlements, does not differ in the three regions ($p = 0.06$): 16, 14 and 17.5% in Europe, West Asia and East Asia, respectively (Fig. 3).

Number of terrapins per water body

The three regions with the highest number of observations, Europe, West Asia, and East Asia (Fig. 1a), have a remarkably higher percentage of water bodies with more than one red-eared slider individual per aquatic site compared with other parts of Eurasia: ($\chi^2 = 100.6$, $df = 6$, $P << 0.001$) (Fig. 2b). The highest portion of such water bodies was observed in East Asia (72.9%); here, the proportion of these water bodies was significantly higher than in Europe, 43.0% ($Z = 8.5$, $P << 0.01$). The mean number of slider individuals per aquatic site was 23.2 ± 9.6 (1–4288; n=490)


a
Habitats
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b
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c
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d
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187 36 1 31 3 11 1
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wintering reproductive attempts successful reproduction populations

Figure 2. Ecological characteristics (left axis, %) and numbers of observations (at the tops of columns) of the red-eared slider *Trachemys scripta elegans* in different parts of Eurasia. **a** habitats: sites outside human settlements ("nature"); urban sites outside recreational zones ("urban sites"); public parks **b** number of individuals per water body (n) **c** body sizes (cm) **d** ecology: wintering; unsuccessful reproductive attempts; successful reproduction; establishment of populations. Colors are explained in the legends.

for Europe; 10.1±2.6 (1–98; n=57) for West Asia; 61.8±31.9 (1–10000; n=318) for East Asia (observations with an estimated number of "several individuals" were excluded from this calculation). Proportion of larger groups increased over the years in Europe (see Suppl. material 5). Here, the greatest numbers (>200 ind. per water body; 1186.4±537.1 (250–4288; n=7)) were reported in the 2000s in Spain (regions of Doñana National Park and Valencia (Perez-Santigosa et al. 2008; Sancho and Lacomba 2013). In East Asia, the greatest number (>200 ind.; 1425.4±860.6 (212–10000; n=11)) were noted in several regions of Japan and China (e.g., Taniguchi et al. 2017; Gong et al. 2018). We are not aware of such large groups of red-eared sliders in other parts of Eurasia. Ignoring these 18 extra-populated water bodies, the mean number of individuals in groups was 15.4±2.5 (2–191; n=485) for Europe, 15.8±4.0 (2–98; n=35) for West Asia and 17.6±1.9 (2–200; n=220) for East Asia. The number of individuals per water body in Europe correlated negatively with latitude in the original/literature dataset even after excluding seven extra-populated (>200 ind.) water bodies in southern regions ($R = -0.13$; $t(N-2) = -2.83$; $N = 485$; $p<0.01$). Such correlation is absent for water bodies in West Asia and East Asia ($R = -0.22$; $t(N-2) = -1.66$; $N = 57$; NS and $R = 0.02$; $t(N-2)=0.33$; $N = 305$; NS, respectively). However, the number of individuals correlates negatively with longitude in West Asia ($R = -0.29$; $t(N-2) = -2.22$; $N = 57$; $p<0.05$) and positively

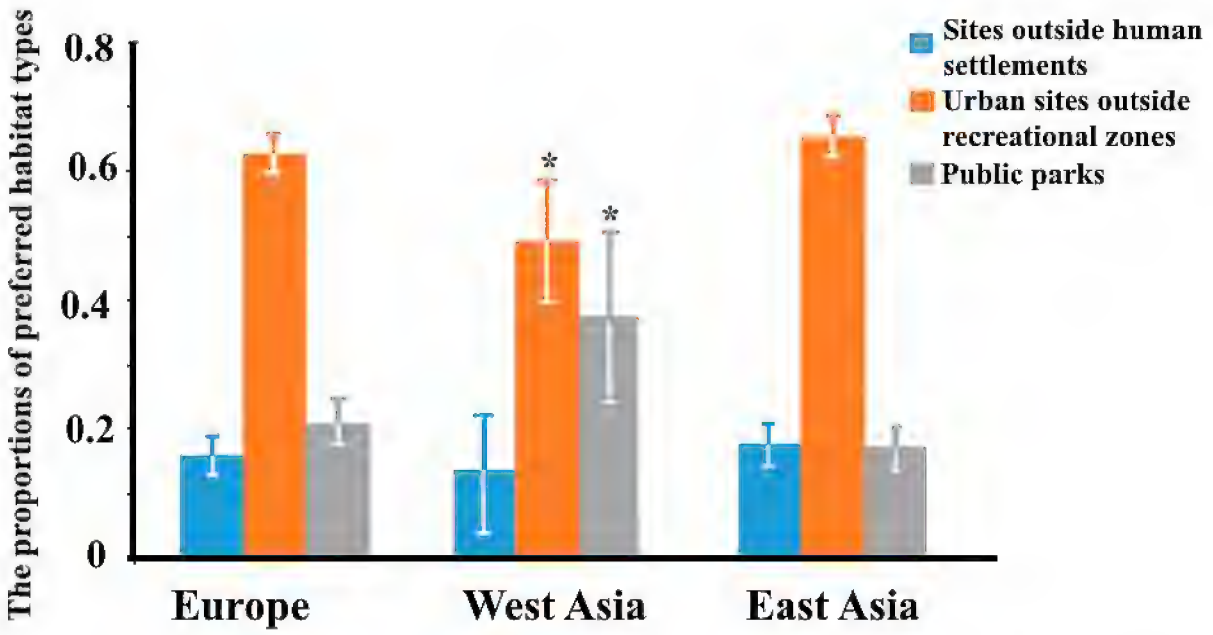

Figure 3. Comparison of the distribution of red-eared sliders among habitats in three different parts of the Eurasian invaded range. See details of habitat coding in Suppl. material 4. Whiskers show 95% Wald's confidence intervals. A multiple comparison of proportions of the same habitat types in different parts of the invaded range was performed using the Chi-square (Biotope 1: 12.5, df = 2, p = 0.001; Biotope 2: 1378.8; df = 2, p < 0.001; Biotope 3: 5.8, df = 2, p = 0.06) and Tukey's Post hoc tests. Significant differences between proportions of the same biotopes in different parts of the range are marked by *.

in East Asia (R = 0.19; t(N–2)=–3.36; N = 305; p<0.001) reflecting association with coastal regions, the Mediterranean coast in West Asia and the Pacific (seas of Pacific Ocean) coast in China.

Body sizes

Diversity and proportions of observations (not water bodies) of various size classes of red-eared slider in parts of Eurasia are presented at Fig. 2c. Below we discuss an assessment of the proportions of water bodies (%) inhabited by individuals of different size classes. Small individuals, with carapace length ≤ 10cm, are detected rarely: in 8.0, 12.5 and 4.6% of water bodies of Europe, West Asia, and East Asia, respectively. Including the category "all sizes", these percentages are 20.8, 33.3 and 70.4%, respectively. Big individuals with carapace length > 15cm were noted in aquatic sites of Europe, West Asia, and East Asia in 31.8, 52.1 and 17.5% or 88.1, 85.4 and 91.2% when including categories "adults" and "all sizes". Very big terrapins (> 20cm) were confirmed in 14.8, 4.2 and 13.7% of areas, respectively. In Europe, the occurrence of small individuals (≤ 10cm; scores 1, 2, 7) negatively correlated with latitude (R = –0.24; t(N–2)= –3.72; N = 236; p<0.001), longitude (R = –0.25; t(N–2)= –4.00; N = 236; p<0.001), positively correlates with number per water body (R = 0.57; t(N–2)= 10.27; N = 215; p<0.001) whereas occurrence of very big individuals (score 5) positively correlated with latitude (R = 0.17; t(N–2)=2.72; N = 236; p<0.01) and negatively correlates with longitude (R = –0.20;

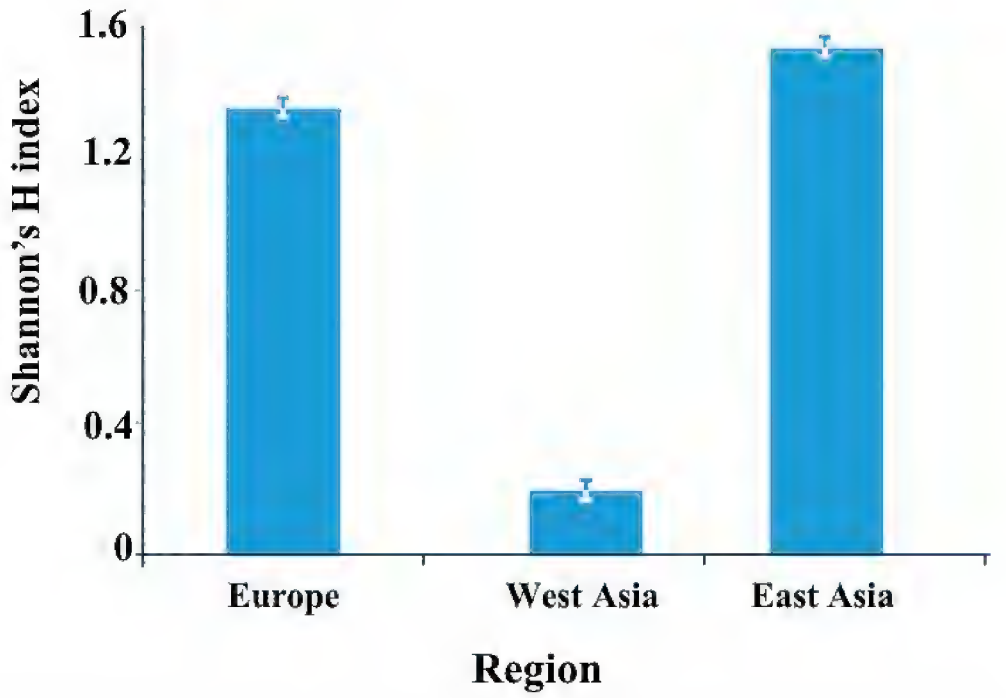

Figure 4. Shannon's index of body size diversity (H) for three different parts of the Eurasian invaded range. Whiskers show 95% Hutcheson's confidence interval.

t(N–2)= –3.09; N = 236; p<0.01). In West Asia, the occurrence of small individuals did not correlate with latitude or longitude (R = 0.16; t(N–2)=1.16; N = 48; NS and R = 0.16; t(N–2)=1.09; N = 48; NS); in East Asia, this size did not correlate with latitude (R = 0.06; t(N–2)=–0.20; N = 240; NS) but positively correlates with longitude R = 0.20; t(N–2)=3.18; N = 240; p<0.01). Therefore, occurrence of small-sized individuals positively correlates with coastal areas. Interestingly, in West Asia, registration of bigger individuals is more typical for water bodies with large groups of red-eared sliders and has increased over time (see Suppl. material 5).

Analysis of indices of the size diversity of terrapin individuals showed that in East Asia, Shannon's index (H = 1.53 ± 0.012) is higher than in Europe (H = 1.38 ± 0.015) and West Asia (H = 0.19 ± 0.032), i.e., body size diversity in East Asia is higher than in the other two parts of the range (Fig. 4). Hutcheson's test suggests the following ranked series for this index: H (East Asia) (t = 51.1; df = 220; p << 0.05) >> H (Europe) (t = 8.87; df = 114; p << 0.05) >> H (West Asia). Although data on the reproductive status in the studied parts of the range are limited, nevertheless, high H index values in East Asia and Europe suggest high size diversity with a sufficient number of both young and mature individuals in these parts of the range for the establishment of populations, if climatic conditions are appropriate.

Ecology

In all parts of Eurasia, except West Asia, the highest number of observations are casual records of red-eared sliders without additional information on ecology. For example, in the most studied regions, Europe and East Asia, the appropriate percentages of casual records are 73.8 and 93.9%, respectively. Multiple cases of unsuccessful reproduction attempts (e.g., egg laying) were registered in Europe and the Trans-Caucasus region,

whereas successful reproduction and even establishment of populations is reported from southern Europe, West Asia, East Asia, and Southeast Asia (Figs 1c, 2d). In European water bodies, successful wintering depended negatively on latitude ($R = –0.23$; $t(N–2)=–6.22$; $N = 671$; $p<0.001$; observations of successful reproduction and establishment of populations were also regarded as wintering points and included in the analysis here and below) and did not correlate with longitude ($R = 0.03$; $t(N–2)=0.68$; $N = 671$; NS) whereas successful wintering in West Asia and East Asia did not depend on latitude ($R = 0.05$; $t(N–2)=0.42$; $N = 59$; NS and $R = 0.01$; $t(N–2)= 0.25$; $N = 586$; NS, respectively). We found such a correlation with longitude for the water bodies of West Asia ($R = –0.49$; $t(N–2)= –4.24$; $N = 59$; $p<0.0$) and East Asia ($R = 0.12$; $t(N–2)= 2.93$; $N = 586$; $p<0.01$). We regarded the relationship between mortality during wintering and latitude using the example of the European part of Russia, a region with a remarkable climatic gradient of thermal conditions. Here, winter mortality was reported for 9.5% of water bodies. We did not find correlations between mortality events and latitude ($R = 0.00$; $t(N–2) = 0.03$; $N = 73$; NS) as dead individuals were registered in both northern (e.g., Saint-Petersburg, Moscow) and southern regions (e.g., Stavropol and Krasnodar territories, Voronezh province of Russia).

In Europe, reproduction is more effective in southwestern regions and positively correlates with terrapin abundance (see Suppl. material 5). In East Asia, reproduction is more successful in the eastern part. The registrations of reproduction have decreased over the years in both Europe and East Asia (see Suppl. material 5). The potential range of reproducing populations of the red-eared slider, as well as the potential range of successful wintering, are presented in Figs 5a, b.

Comparison of the mean values of the predictor variables shows that the niche centroids of the species in East Asia are characterized by relatively high values of mean air temperature in the warm season ($T = 26.01 \pm 0.46$ °C, $n = 35$), precipitation ($W = 676.4 \pm 15.4$, mm), climate moisture index ($Mi = 0.4 \pm 0.03$), and total temperature above 0 °C ($SigmaT = 7.78 * 10^4 \pm 3207$ °C) (Fig. 6). Some niche centroids in West Asia occupy an intermediate position ($T = 23.4 \pm 0.49$ °C; $n = 31$; $SigmaT = 5.868 * 10^4 \pm 3408$ °C; $n = 31$) compared to centroids in Europe and East Asia. The moisture index in the West Asian part of the range ($Mi = -0.33 \pm 0.03$; $n = 31$) is significantly lower than in East Asia, but does not differ from Europe ($Mi = -0.27 \pm 0.02$, $n = 75$). Concerning precipitation in the warm season, the niche of the red-eared slider in West Asia is characterized by the lowest precipitation ($W = 82.3 \pm 16.7$ mm; $n = 31$). The centroids of temperature ($T = 19.3 \pm 0.32$ °C, $n = 75$) and the sum of temperatures ($SigmaT = 3.671 * 104 \pm 2191$ °C, $n = 75$) in Europe are characterized by the lowest values, do not differ in the humidity index from the West Asian part of the range, and occupy an intermediate position in terms of precipitation in the warm season of the year. The centroids of niches in East Asia differ significantly from two other analyzed parts of the range for all studied predictor variables (Fig. 6). Comparison of the mean values of the Log-transformed predictor variables using GLM ANOVA is presented in Suppl. material 8: fig. S4. It can be seen that Fig. 6 and Suppl. material 8: fig. S4 similarly display niche centroid positions across all predictor variables. The normal

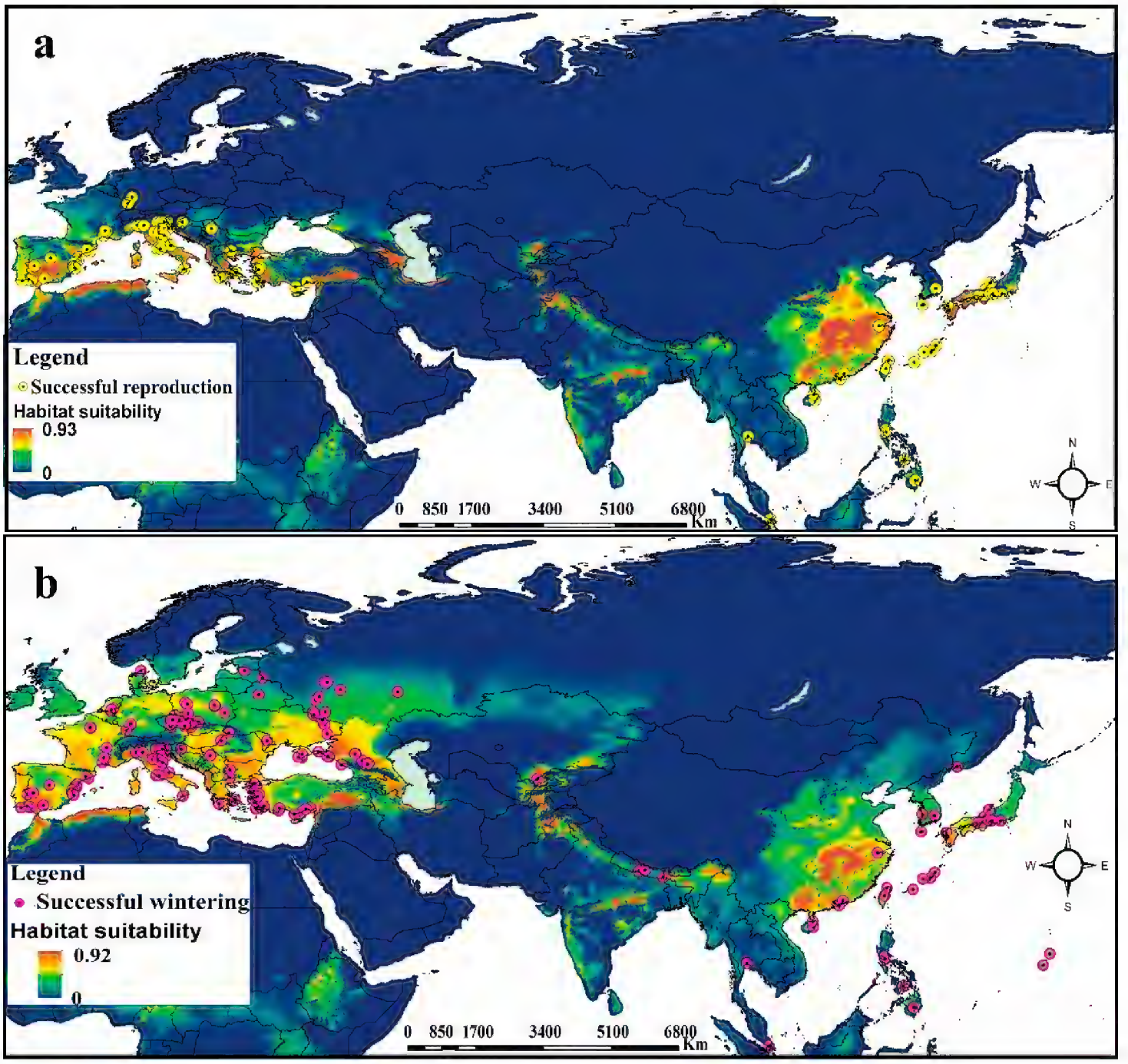

Figure 5. Potential distribution of the red-eared slider *Trachemys scripta elegans,* created with MaxEnt analysis of climatic requirements. **a** potential range of successful reproduction. Species Distribution Model has been built based on records of the native range of the red-eared slider within Northern America and records of successful reproduction and established populations within Eurasia (which are shown by yellow points) **b** potential range of successful wintering. Species Distribution Model has been built based on records used for Fig. 5a with the addition of records with confirmed successful wintering within Eurasia (which are shown by pink points).

distribution of GLM ANOVA residuals after Log-transformation for all variables suggests that conclusions regarding the significance of the centroid difference, established without data transformation, are correct.

A comparative analysis of the parameters of reproductive efforts in Eurasia showed that centroids 2 and 3 (wintering and egg laying) significantly differ from 4 and 5 (successful reproduction and establishment of populations) (Fig. 7). We combined centroids of 2 and 3 and presented them as level I and combined 4 and 5 as level II. The appropriate mean values and ranges of values for level I (n = 100) in Eurasia are as follows: T = 20.6 (range 19.1–21.21) °C; W = 298.5 (206.3–390.7) mm;

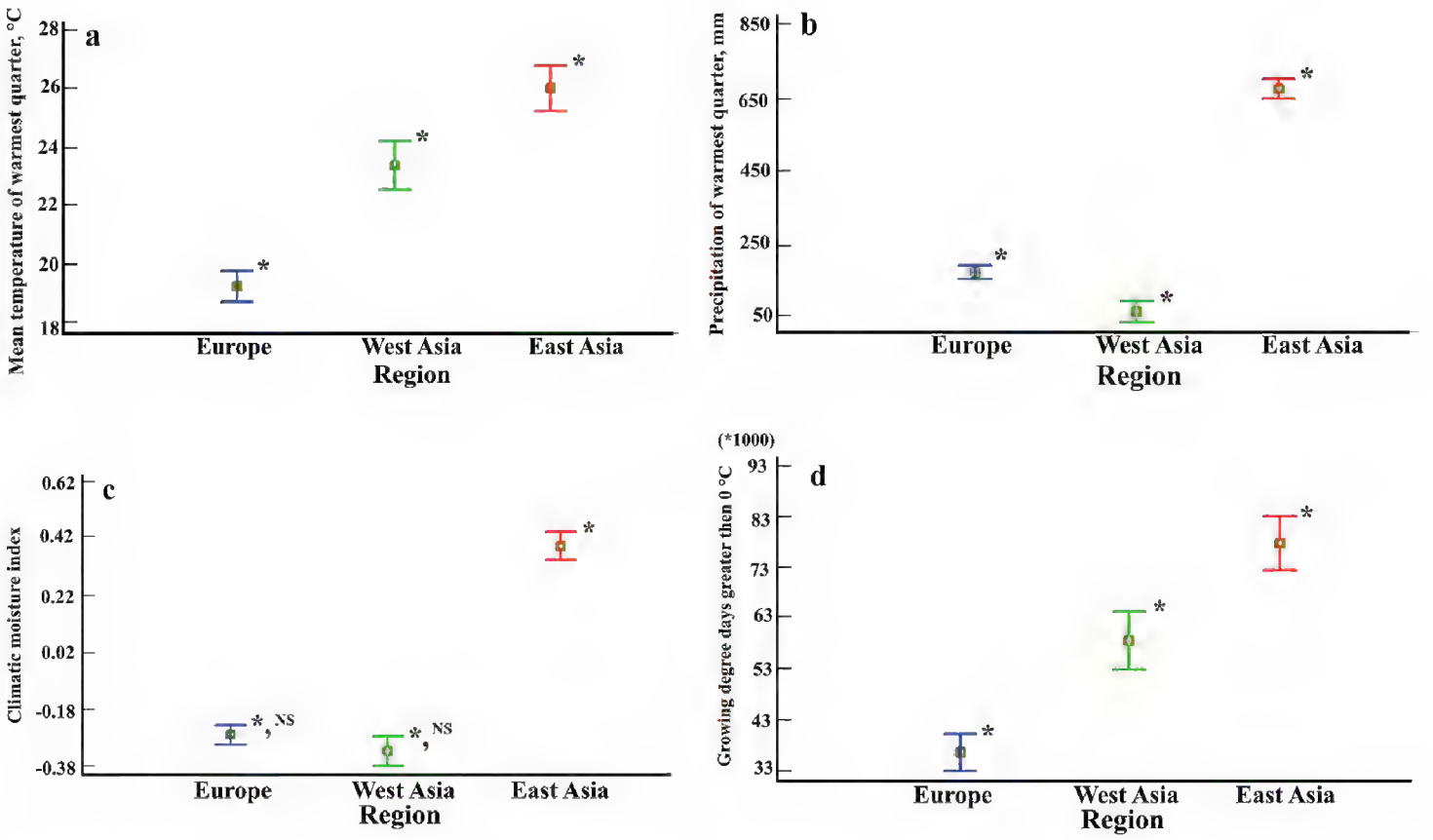

Figure 6. Comparison of mean values (± 95% Tukey HSD confidence intervals) of the main predictor variables of terrapin habitats in different parts of the invaded range. The results of one factor ANOVA based on General Linear Model are presented. The GLM ANOVA tested the main effects of regions: **a** $F = 78.31$, df = 2, $p < 0.01$ **b** $F = 424.21$, df = 2, $P < 0.01$ **c** $F = 196.42$, df = 2, $p < 0.01$ **d** $F = 58.62$, df = 2, $p < 0.01$ (F is Tukey HSD test; P-value is given for the factor effects). Significant differences of means according to Post hoc Tukey HSD test are marked by *. Absence of significant differences is marked as NS, i.e., values for Europe and West Asia do not differ from each other on Fig. 6c. Records with ecological characteristics 2–5 (see Methods) were used (so, we ignored casual records for this analysis).

Mi = -0.17 (-0.31 – -0.04); SigmaT = $4.152*10^4$ ($3.22*10^4$–$5.084*10^4$) °C and for level II (n = 41) are: T = 25.5 (24.4–26.7) °C; W=521.3 (410.2–631.0) mm; Mi = 0.15 (0.08–0.3); SigmaT = $7.294*10^4$ ($6.185*10^4$–$8.404*10^4$) °C. A comparative analysis of the parameters of reproductive efforts in Eurasia with Log-transformed data is presented in Suppl. material 8: fig. S4. Importantly, the results of comparing the niche centroids did not differ regardless of whether the original data are Log-transformed or not. Since the residuals of the GLM ANOVA models after Log-transformation of the predictor variables did not differ from the normal distribution, we therefore limited our comparison to mean values only.

Discussion

Spatio-temporal dynamics

The earliest reports of the red-eared slider in outdoor water bodies of Eurasia originate from the late 1960s – early 1970s in Europe (Rumburk, Czech Republic), where this animal was recorded in 1968 (Moravec and Široký 2006), and East Asia (Okinawa

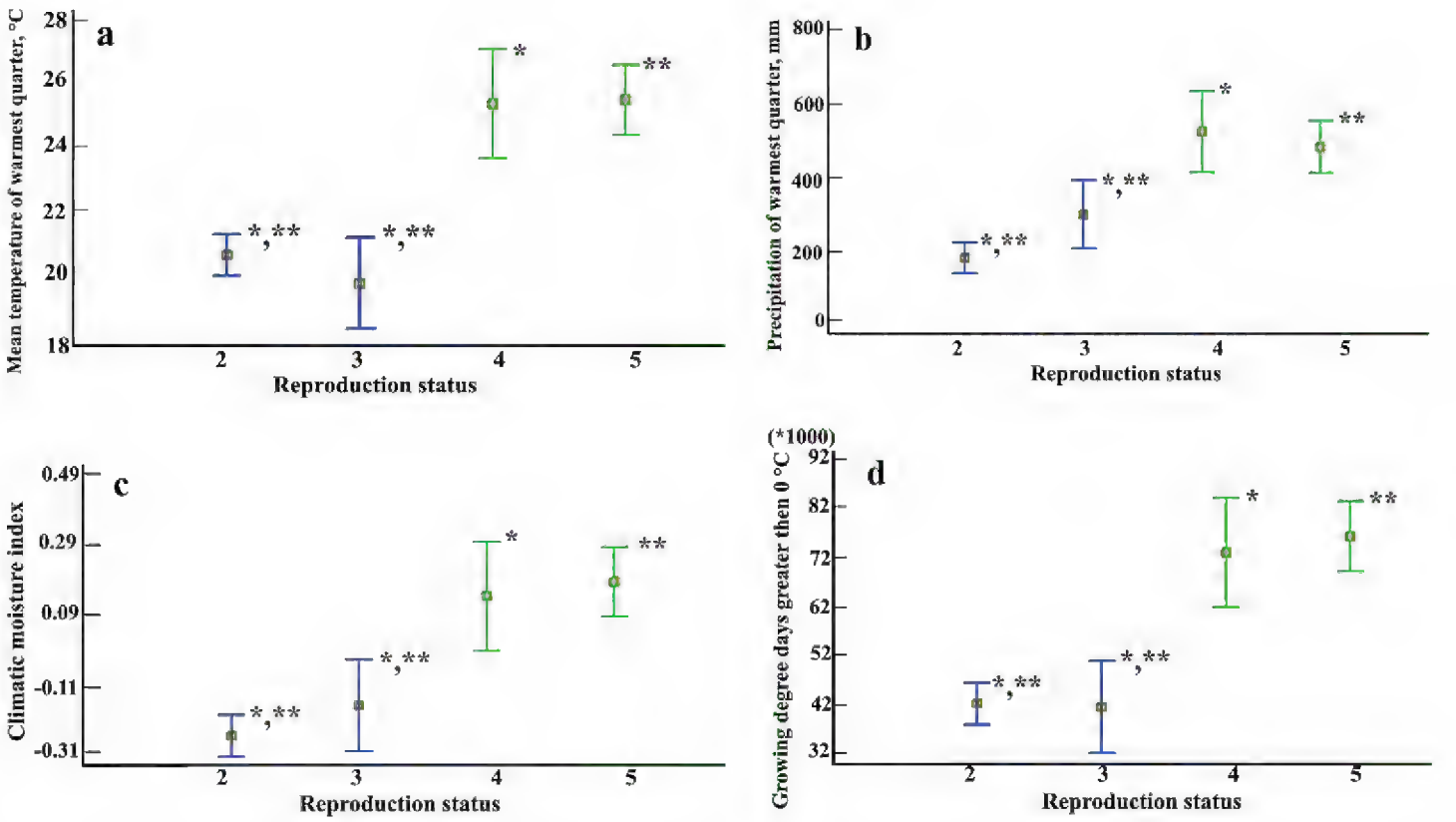

Figure 7. Comparison of mean values (± 95% Tukey HSD confidence intervals) of main predictor variables of terrapin habitats for records with different ecological/reproductive statuses. The results of one factor ANOVA based on General Linear Model (GLM) are presented. The GLM ANOVA tested the main effects of reproduction status (where 2 is confirmed successful overwintering; 3 is unsuccessful reproduction attempts, 4 is confirmed successful reproduction, 5 is established population): **a** F=23.5, df = 3, $p < 0.01$ **b** F = 20.92, df = 3, $p < 0.01$ **c** F = 19.7, df = 3, $p < 0.01$ **d** F = 24.4, df = 3, $p < 0.01$ (F is Tukey HSD test; p value is given for the factor effects). Statistically significant differences of means according to Post hoc Tukey HSD test between 4 and 2, 3 (separately) is marked by *; statistically significant differences of means between 5 and 2, 3 (separately) is marked by **. We did not compare means of categories 2 and 3 as they are rather similar. The same is true for 4 and 5.

Island, Japan), with detection in 1972 (Shimazu 2015). Soon after, this alien was also first detected in West Asia (Bethlehem, Israel) in 1975 (Bouskila 1986). Up to the beginning of 21st century, outdoor occurrence of the species under study was restricted mainly to Europe and East Asia, with less frequent reports in West Asia and Southeast Asia (Fig. 1b). Contrary to the invasion histories of some "classical" invaders such as the insect *Agrilus planipennis* or fish *Perccottus glenii* (e.g., Reshetnikov and Ficetola 2011; Orlova-Bienkowskaja et al. 2020), colonization by the red-eared slider did not have a limited number of initial introductions which became sources of secondary distribution with the potential establishment of invaded subranges. The geographical expansion of this reptile was driven by massive propagule pressure in different regions over the huge territory of Eurasia. Nevertheless, Europe and East Asia were the regions with earliest and greatest dissemination compared with other parts of the continent (Fig. 1b). To date, this terrapin species is present in almost all countries of Eurasia (Fig. 1a). It has been reported from 68 Eurasian countries. The original list of Eurasian countries colonized by red-eared slider is available in the Suppl. material 9.

Invasion ecology

Of course, data on ecological characteristics of the red-eared slider for some water bodies may be absent due to lack of appropriate observations. Nevertheless, our large-scale spatio-temporal approach (invasion within all of Eurasia during a 50-year period) reduces possible inaccuracies and allows us to reconstruct the invasion process within the studied continent. Our comprehensive database of primary data allowed us to compare ecological features of the red-eared slider in different parts of Eurasia. We found that the ecological niche of reproductive groups of the red-eared slider in East Asia differs from those in Europe and West Asia in terms of thermal energy and moisture (Fig. 6). This may be explained by the absence of the whole range of appropriate favorable environmental conditions in Europe and West Asia. Breeding groups of this invader are likely to occupy habitats with more favorable climatic conditions in East Asia, with higher temperature and humidity compared with other parts of Eurasia (Fig. 6). Despite the absence of appropriate records of reproductive success, our modelling confirms the existence of large territories favorable for reproduction in non-coastal regions of China and Azerbaijan, and southern Turkey, as well as limited regions of several other countries, including Kazakhstan (south), Iran (north), India, Nepal and others (Fig. 5).

Importantly, the red-eared slider inhabits mainly urban and rural environments (Fig. 2d) because the principal invasion vector is pet release (Semenov 2010; Banha et al. 2017). It is not surprising that synanthropic groups of this terrapin are more abundant, as it has been shown for Europe and West Asia. However, the distribution of red-eared sliders is not limited by territories of human settlements, where this terrapin is often used for decoration of ponds. This invader has already been detected in natural environments, i.e., outside human settlements, in most parts of Eurasia (Fig. 2a). In Europe and East Asia, the proportion of records in natural habitats reaches 16–17%. In West Asia, records in natural water bodies amount 13.7%. This reflects the unavoidable dispersion of these animals from points of initial introductions (e.g., urban and rural ponds) to other places. Pet terrapins can migrate to natural habitats both through the hydrological network and over land; however, at least in some cases, they were introduced directly into nature (e.g., Doñana National Park, Perez-Santigosa et al. 2008).

Recorded red-eared slider numbers may entirely (in regions without reproduction) or partly (in regions with reproduction) reflect past human activities, i.e., accumulation of human-released slider individuals, a phenomenon defined as "invasion debt" (Essl et al. 2011). Commonly, aquatic sites with red-eared sliders have one terrapin individual per water body, however the number varies and mean values are tens of individuals for different parts of Eurasia, with the highest abundance in East Asia, where the mean value is 62 individuals per water body. High numbers and biomass of this alien hydrobiont produces risks for native freshwater ecosystems (Cadi and Joly 2004; Lee et al. 2016; Salerno and van den Burg 2021). In Eurasia, the number of sliders

may reach thousands of individuals per aquatic site (Perez-Santigosa et al. 2008; Sancho and Lacomba 2013; Taniguchi et al. 2017; Gong et al. 2018). Therefore, this alien reptile became a target of eradication campaigns in this region from the early 2000s (e.g., Sancho and Lacomba 2013). However, despite possible local success, our review did not reveal any signs of decrease in terrapin abundance over the years, or signs of decreasing geographical range on the all-Eurasian scale (see Suppl. material 5; Fig. 1b).

Our results show a higher density of records of the slider in Europe and East Asia (Fig. 1b). The density of records may correlate positively with the density of human population (Banha et al. 2017). Propagule pressure (the number of release events) is often positively correlated with human population density, whereas survival and reproductive success of terrapins depends mainly on climate conditions, i.e., fundamental niche. Therefore, both climatic and anthropic factors are important to this terrapin for invasion. Analyzing invasion ecology, we found that many characteristics of invasion success (e.g., higher portion of inhabited natural water bodies, higher number of individuals per water body, successful overwintering, presence of juvenile individuals, successful reproduction and establishment of populations) tend to be present in coastal regions, such as the Mediterranean coast of southern Europe, the western part of West Asia, the Pacific coast of East Asia and islands. The coastal regions could have milder thermic and more favorable humidity regimes, which are important for the reproduction of this reptile.

Reproductive success depends on several key environmental parameters (Fig. 7). Assessing bioclimatic differences between presence and reproduction occurrence is important (Ficetola et al. 2009; Heidy Kikillus et al. 2010). For example, despite a great number of occurrence records in Europe, the establishment of self-sustained populations of this terrapin has been proved only for southern regions of Europe in Spain, Italy and southern France (Cadi et al. 2004; Perez-Santigosa et al. 2008; Ficetola et al. 2009; Crescente et al. 2014). On the other hand, specialists report successful reproduction in a larger number of localities and do not exclude the possibility of established populations in Portugal, Greece, Croatia, Slovenia, and Serbia, in locations where a similar Mediterranean climate is prevalent (Bruekers et al. 2006; Đorđević and Anđelković 2015; Standfuss et al. 2016; Koren et al. 2018; Martins et al. 2018; Tzoras et al. 2018; Urošević et al. 2019; our data). Of course, some observed groups of terrapin may be at different stages of invasion debt (Essl et al. 2011), with potential establishment of populations in the future, after the accumulation of human-released individuals of reproductive age and/or due to future climate alterations. In regions with suboptimal climatic conditions, e.g., lowland territories of Switzerland and Austria, and south Germany, the red-eared slider can also successfully reproduce but more rarely, only in some very hot summers (Bringsøe 2001; Wüthrich 2004; Pieh and Laufer 2006; Kleewein 2015; Schradin 2020). However, some above-mentioned data originate from open areas of zoos (Wüthrich 2004; Kleewein 2015), not from natural landscapes. Additionally, sometimes records of hatchlings from urban park ponds (Bringsøe 2001; Pieh and Laufer 2006) are difficult to separate from bought and released young-of-the-year juveniles (see facts and discussion in: Semenov 2010;

Ficetola et al. 2012). Registration of reproductive efforts, i.e., female egg-laying behavior, is the least informative ecological parameter because it characterizes neither success of reproduction, nor physiological adaptation to local geographical conditions. Therefore, despite multiple registrations of unsuccessful reproduction efforts in some more northern countries of Europe, e.g., Belgium, the Netherlands, Denmark, Czech Republic, and Poland (Bringsøe 2001; Najbar 2001; Herder 2007; Brejcha et al. 2010; Verbelen 2021), temperature conditions in those countries are, possibly, much less favorable for successful development of embryos at the present time (Fig. 5a).

In the current analysis (Fig. 1c), the northernmost countries of successful reproduction of this reptile in West Asia and East Asia are Turkey, Japan and Republic of Korea (Çiçek and Ayaz 2015; Taniguchi et al. 2017; Koo and Sung 2019). However, climatic conditions of even some more southern regions of Asia seem to be unsuitable for reproduction (Fig. 5a). We propose that cold mountain climates and lack of soil humidity of some other regions inhibit reproduction of the studied reptile. Indeed, the eggs of *T. scripta* have a skin envelope (Cagle 1944) and are less protected against desiccation compared with hard-shell eggs of some other terrapins (Tucker et al. 1998). Multi-year monitoring of groups of *T. s. elegans* individuals in an arid region do not reveal successful development of naturally laid eggs under extremely dry conditions (Drost et al. 2021), which further supports our hypothesis. Importantly, sex determination of embryos of the red-eared slider is temperature-dependent (Tucker et al. 2008). Only males appear under low incubation temperature; this feature is regarded as a possible limitation for the establishment of populations in northern regions, with insufficient thermal conditions for the production of both sexes (Cadi and Joly 2004; Heidy Kikillus et al. 2010). Additionally, red-eared sliders can inhabit thermal or heated water bodies with special microclimatic conditions and can benefit from a higher reproduction potential due to earlier maturation with greater body sizes, earlier start of the nesting season and larger clutch sizes (Thornhill 1982). For example, hatchlings of *T. s. elegans* may be recorded in thermal springs (e.g., in Bulgaria, Kornilev et al. 2020) outside areas of proven reproduction of this species. Among our dataset, the northernmost records of this slider in North Asia (e.g., West Siberia and Kamchatka peninsula) with rather severe climates are restricted to thermal reservoirs; however we have not found confirmation of survival and reproductive success in those localities (Fig. 1c).

Paradoxical expansion without reproduction

The results of all the species distribution models have some differences due to variations in datasets and climatic variable sets used. The calculated reproductive range of the red-eared slider in Eurasia in our study (Fig. 5a) is based on the most comprehensive dataset and significantly updates some earlier SDM prognoses of successful reproduction for this terrapin (Rödder et al. 2009; Heidy Kikillus et al. 2010). For instance, our model excludes England as an area favorable for reproduction. Analysis of the literature indirectly suggests our model may be suitable because there have not yet been reports confirming successful reproduction of the studied terrapin in England.

Nevertheless, current geographical occurrence of this terrapin (Fig. 1b) is not limited to areas climatically suitable for successful reproduction (Fig. 5a). As the main invasion vector and driver is pet releases (García-Díaz et al. 2015), the geography of initial introductions does not depend on climate features. Despite the reproduction of this terrapin being restricted to a few regions of Eurasia with comparatively high summer temperatures and sufficient air humidity (Fig. 1c), the released red-eared slider tolerates a wide range of temperatures and does not depend on air humidity around recipient water bodies. Individuals of this species activate their feeding behavior when water temperature is above 10 °C (Parmenter 1980). Many lowland freshwater aquatic sites of Eurasia reach such thermal conditions during summer. So, this terrapin becomes included in the food webs of local ecosystems immediately after its release. It is assumed that even a few big individuals of red-eared slider are capable of damaging low-component ecosystems of small isolated water bodies like artificial ponds (Semenov 2010). However, numbers of this invader often reach much higher values in Eurasian water bodies (Fig. 2b). Thus, this reptile demonstrates wide expansion without establishment of populations. Recruitment of new individuals to "pseudopopulations" of the red-eared slider takes place due to additional releases. Once released, individuals of this terrapin may inhabit a water body up to 30–31 years (Frazer et al. 1990; Castanet 1994). As a result, despite the absence of reproduction in the most regions of Eurasia (Fig. 5a), its occurrence area has enlarged considerably from the end of 1960s to the late 2010s and presently covers a considerable portion of Eurasia (Fig. 1b).

Conditional invasion

The invasive status of a species assumes 1) naturalization, i.e., establishment of populations, and 2) remarkable negative impact on native species/ecosystems (Cadi et al. 2004; Standfuss et al. 2016). Thus, invasive status, *sensu stricto*, of this reptile is not confirmed for the majority of Eurasian countries because established populations are registered only in a few regions (Fig. 1c). However, keeping in mind its abnormally high propagule pressure (García-Díaz et al. 2015), ability to survive under suboptimal conditions (Willmore and Storey 1997), long life duration (Castanet 1994), increasing numbers (without reproduction) due to progressive cases of releases and continuing geographical expansion, this aquatic reptile has acquired invasive status without the establishment of reproducing populations in areas where it can survive for more than one year. Because of the lack of such an important feature as establishment of populations, this new type of invasion may be defined as a "conditional invasion". This may be applied to this reptile within the area of successful wintering excluding the area of successful reproduction.

Wintering range as an important criterion for risk assessment

Successful wintering is registered for all parts of the continent (Figs 1c, 2d, 5b). The only hitherto known confirmation of wintering in North Asia is restricted to the Far

East region of Russia, with its mild marine climate. We do not have confirmation of successful overwintering in other regions of North Asia, which are characterized by a severe continental climate with low winter temperatures. Interestingly, during severe winters with subzero temperatures in southern regions, some individuals may die but others can survive in the same water body (Stoyanov 2015). On the other hand, wintering success can differ in different years depending on weather conditions (Reshetnikov and Sokolov 2020). Climatic thresholds for successful wintering may be explained by physiological restrictions. Red-eared sliders usually hibernate on the bottom of water bodies and the aquatic environment reliably protects them against subzero temperatures if a layer of water remains between the ice and bottom of the water body. Importantly, during hibernation, this terrapin can tolerate near-zero positive temperatures, as well as considerable deficit and even short-term absence of oxygen (Ultsch 2006); therefore, this species is sometimes regarded as a facultative anaerobe (Willmore and Storey 1997). Theoretically, crucial criteria for survival may be: 1) duration of winter ice-covering period because the red-eared slider does not survive if anoxic conditions last longer than 44–50 days (Ultsch 2006); 2) number of days with water temperature above 10 °C in the warm period, impacting the condition of the terrapin body prior to wintering, e.g., lipid reserve, necessary for long hibernation without exogenous feeding. Such body condition is difficult to reach in northern and mountainous regions with a brief warm season, as well as in internal areas of the continent with a severe continental climate. In such regions, climatic limitations of successful wintering may be non-direct: this animal survives under low water temperatures, but is deprived of the necessary physiological reserves that might prepare it to tolerate a prolonged period of unfavorable conditions. Calculated limitations of wintering in some regions in the south of Asia (Fig. 5b) are less understandable. Theoretically, the main limiting factors may be related to high temperatures and water deficit, especially for vast arid areas of Saudi Arabia, Yemen, Oman, Iraq and Afghanistan. However, we cannot exclude year-round existence of the red-eared slider in oases with permanent aquatic sites.

We propose the "range of successful wintering" as a territory at risk for true invasion as well as for conditional invasion. This non-standard (for a reptile) characteristic, i.e., wintering range, must be taken in account when planning eradication campaigns or other measures of control of the red-eared slider.

Conclusions

The geographical expansion of the red-eared slider started in the 1960–1970s from two opposite sides of Eurasia, i.e., Europe and East Asia, and was driven by massive propagule pressure in different regions over its huge territory. The invasive range of this terrapin enlarged gradually in Eurasia up to the beginning of the 2020s covering 68 Eurasian countries. In particular, we report original data outlining recent first detections of this alien terrapin in the following countries: Bangladesh, Georgia, Kazakhstan, Kyrgyzstan, Mongolia, Nepal, Pakistan, Tajikistan, as well as Russian Siberia (drainages of

rivers Ob and Yenisei). Regions of successful reproduction of this ectotherm in Eurasia are well-predictable on the basis of climatic features of the native geographic range but may be altered because of progressing global climate change. Analyses of invasion ecology confirm that coastal regions and islands show the most prominent expression of diverse signs of invasion success in terms of a higher portion of inhabited natural water bodies, higher number of individuals per water body, successful overwintering, occurrence of juvenile individuals, successful reproduction, and establishment of populations. Notably, a great number of established groups of this reptile in different regions of Eurasia do not meet the conditions for successful reproduction.

In this pet terrapin we have an excellent but rare example of wide geographic expansion without the establishment of (reproducing) populations but through the recruitment of new individuals to growing (non-reproducing) pseudopopulations due to additional releases. Therefore, we highlight the significance of the wintering range. This range must be taken in account when planning measures of control of this invader because non-reproducing groups of this terrapin may become a significant component of freshwater ecosystems with impact on native species. Thus, a cost-effective conservation strategy against the red-eared slider in large countries with a variety of climatic zones may differ for three geographical areas: 1) area of true invasion (within potential reproduction range), 2) area of conditional invasion (within potential wintering range but outside potential reproduction range), and 3) area without potential for reproduction and wintering. Nevertheless, some protective measures (i.e., banning of import and trade) are effective only on an all-country level and therefore must be applied at national levels. Finally, we encourage further accumulation of empirical knowledge on the invasion ecology of the red-eared slider in newly-invaded regions, especially in North Asia and South Asia, to establish a deeper understanding of its adaptive limits and role in Eurasian native ecosystems.

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Supplementary material 1

List of literature sources with records of red-eared slider in Eurasia

Authors: Andrey N. Reshetnikov et al.

Data type: Pdf file

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Supplementary material 2

Eurasian subregions as accepted in the current article
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Supplementary material 3

Data base of georeferenced records of *Trachemys scripta elegans* in Eurasia
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Supplementary material 4

Coding of collected field data
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Supplementary material 5

Correlation matrix for ecological and other parameters of the red-eared slider *Trachemys scripta elegans* in water bodies of Europe (a), West Asia (b) and East Asia (c)
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Supplementary material 6

Locations of the training areas based on the available occurrence records
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Supplementary material 7

Evaluation metrics for MaxEnt models made across a range of feature-class combinations and regularization multipliers
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Supplementary material 8

Comparison of mean values of the Log-transformed predictor variables

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Supplementary material 9

Original list of 68 Eurasian countries colonized by the red-eared slider *Trachemys scripta elegans*

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Supplementary material 10

Additional list of 52 persons who kindly provided their observations of red-eared sliders in open water bodies of Eurasia

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